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SYMPOSIUM ON STABILITY IN DYNAMIC MICROBIAL SYSTEMS

V. THE THEORETICAL BASES FOR CLASSIFICATION OF THE FUNGI IMPERFECTI

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ABSTRACT

Considerable revisionary effort is currently being directed toward the systematics of the Fungi Imperfecti and, in particular, toward the classification of the hyphomycetous molds. The classical system of Saccardo, with its emphasis on relatively superficial morphological and ecological characters, provides a classification niche for every known fungus but often is useless in revealing taxonomic relationships based on characters more nearly fundamental than habit, color, or spore septation. A discussion of the requirements of a new, information-rich classification is used to introduce a review of recent systematic revisions based on methods of asexual spore production observed among these fungi.

INTRODUCTION

THE practicing taxonomic mycologist associated with a culture collection commonly bears the responsibility of having on hand or of knowing where to locate particular fungus isolates and information on them, and of attempting to estimate the reliability and pertinence of this information. Always involved in such estimates is a consideration of the degree of taxonomic sophistication exhibited by the author of the information. In other words, how well has he succeeded in categorizing his fungus in an available classification system? and is the chosen classification system the one which currently yields the greatest possible amount of additional information? J. Heslop-Harrison (1962) may be quoted here to advantage: "There can be few biologists who would not accept as one of the primary functions of biological systematics the production of a general classification of living things possessing at once the greatest possible content of information and the maximum convenience in use. Whatever other function may be attributed to taxonomy . . . this one, the creation of a data storage and retrieval agency, is surely the inescapable one." (p. 14).

This opinion of Heslop-Harrison and the method of operation of the taxonomic microbiologist, in weighing a contributor's classification sense in the same balance with his information, both bear the stigma of pragmatism. There is no insistence here on a pure taxonomy derived from phylogenetic relationships. For the mycologist it is a practical approach, tinged for many of us with the gray hope, for many others with the unstable illusion, that the classifications we are using coincide in significant areas with a taxonomy related to a predominance of fundamental characteristics.

Taxonomy of Microfungi

To this point I have attempted to maintain a distinction in usage between the two words "classification" and "taxonomy." *Classification* is used to designate any systematic arrangement

of organisms in groups or categories based upon some definite scheme. *Taxonomy* is a special sort of classification of organisms according to their natural relationships.

Mycological classifications may be so simple and unenlightening as stacking all the black fungi in one pile, all the yellow ones in another, the red ones elsewhere, and so forth. Or a classification may be so perceptive as to recognize that no amount of juggling other characters has been able to shake our conclusion that the sexually-derived ascus is a fundamental character of enormous numbers of fungi, and that its presence indicates a taxonomically significant relationship among those organisms which produce it.

All microbiologists are involved in classification of microorganisms to some extent or know where they can apply for help. Discussions of the theories of classification can be based on mutual experience and information. On the other hand, the body of observations relevant to a true taxonomy in any group of microorganisms is meager. Taxonomic theories are available to us but their foundations are on quicksand.

Taxonomy of Other Groups of Microorganisms

Pessimistic views on the state of fungus taxonomy can be transferred justifiably to other groups of microorganisms. A few modern specialists in those groups speak as follows, in quotation or in paraphrase.

J. O. Corliss (1962), on the taxonomy of protozoa:

> In general the protozoologist is still in the dark ages of taxonomy's stage one, namely, the production of conventional descriptions of species and groups of species, although for practical reasons he must attempt a bit of taxonomic synthesis, thus dealing with schemes of natural classification embracing all levels in the taxonomic hierarchy. (p. 37).

On virus classification, N. W. Pirie (1962) remarks:

> "There is no reason to think that viruses are related, as plants and animals are generally held to be, by an evolutionary sequence. . . . (p. 376). There is little hope of bringing all the viruses into one comprehensive system that has scientific validity. All that will probably be achieved is the establishment of some groups of viruses within which relationships can be defined, but the groups may remain unrelated to one another." (p. 377).

S. T. Cowan (1962), in discussing the validity of considering that our present hierarchical system of bacterial classification (i.e., order, family, genus, species) actually reveals or represents natural phylogenetic relationships, concludes as follows:

> "We can say with confidence that microbes cannot, on present knowledge, be arranged in a hierarchical system to show their phylogeny. The great unravelling of microbial relations awaits the results of more crossing experiments and it is to the geneticists that we must look for future advances in phylogeny." (p. 451).

For further elaboration of the condition of classification systems now in use for groups of microorganisms other than the fungi, let me refer you to a published volume of collected papers which are the sources of the quotations above and which cover with remarkable fullness and clarity many of the problems barely mentioned here (Ainsworth and Sneath, 1962).

CLASSICAL CLASSIFICATIONS OF FUNGI

Classifications of the microfungi, like those of most other kinds of microorganisms, took their origins in relatively superficial morphological and ecological observations. Morphology of the microscopic fungi, particularly that of the sporulation apparatus, always has formed the unifying base of our classification systems. Perhaps some combination of physiological and chemical factors would support a better system of natural relationships; however, the myco-physiologist or biochemist applying himself to this possibility on a comprehensive scale is a rare bird — if, indeed, he exists at all. So little is known about even the most superficial physiological aspects of the great majority of fungi that a classification based on such characters today would be about as usable as are the mycological manuals of the early 1800's. We can begin to propose a major revision on other than morphological bases only when we achieve for many fungi a *spread* of information approximating the *depth* of information we

now have on our handful of laboratory and production pets.

In historical progression, the student of microfungi has had available to him the classifications of the early and middle 19th century (Corda, 1837–1854; Fries, 1821–1832; Persoon, 1801); those of the late 19th and early 20th centuries (Costantin, 1888; Saccardo, 1882–1931; Vuillemin, 1910a,b, 1911); and one of the mid-20th century (Hughes, 1953).

Pre-Saccardoan Systematics

The early 19th century three-volume *Systema Mycologicum* (Fries, 1821–1832) contains a larger number of categorized descriptions of microfungi than does any other publication of that period. This early cataloguing attempt reflected a comprehensive knowledge of the mycological literature of that day, and from that vantage point it exerted tremendous influence in the area of fungus classification. However, Fries held a very low opinion of the microscopic molds in general, did not spend much time studying them, and derived his morphologic-ecologic classification to a great extent from published observations which often were as poor as or worse than his own. Microscopes were primitive, so that even the best observations on morphology were superficial. The resultant comparisons and classification opinions of that period are the historical fiction of today.

As optical equipment improved, so too the number of hyphal and spore characters which could be examined, measured, compared, and categorized increased. In the mid-19th century, Corda's critical eye and fastidious pen combined in producing excellent illustrations and descriptions of microscopic fungi (Corda, 1837–1854). He paid close attention to the details of his material and to a great extent influenced the interest of other mycologists in the microscopic morphology of spores and of the sporulation apparatus. Corda's level of accuracy was high, and the immediate value of the several volumes of his work probably lay in the field of identification. In addition, the fact that he and later mycologists could distinguish and characterize so well the shapes, septation, ornamentation, and arrangements of sporulating structures emphasized the possibility of erecting a classification system on the basis of such microscopic features.

Concurrently there developed another area of fungal characterization, namely phytopathology, with medical mycology later making its own contributions to fungal taxonomy. Unfortunately, the idea arose and became firmly entrenched that each host-fungus relationship was unique and that morphologically identical fungi should be classified separately if they occurred on different hosts. This idea, also unfortunately, never has left us, and mycological literature continues to be crammed with thousands of fungus names which can be related to other pertinent information only after the hosts or substrates of the fungi have been identified.

Saccardoan Classification

The tens of thousands of microfungi which had been described and named by 1870 made some sort of comprehensive classification a practical necessity. P. A. Saccardo, in the 1870's and 1880's, devised a master plan of classification for all the fungi. In the series of 25 volumes of his *Sylloge Fungorum* (Saccardo et al., 1882–1931), he and his colleagues managed to catalogue and to dispose in his system more than 80,000 fungus descriptions. Saccardo's major contribution to classification of the Fungi Imperfecti was the development of an interlocking series of morphological categories of increasing complexity. His primary divisions for this group of fungi were defined by the structure of the hyphal complex with which spores were associated (Fig. 1): the Sphaeropsidales, with the sporulating apparatus enclosed within a definite wall, the pycnidium; the Melanconiales, with sporulation arising from a parenchymatic stroma, the acervulus; and the Hyphomycetales, with spores (when present) produced on various arrangements of hyphae, but these neither enclosed in pycnidia nor based on a stroma. Laid across these parallel divisions was a double network of color and complexity of shape and septation of spores (Fig. 2).

Saccardo did not actually use all of these theoretically available secondary categories because representative fungi for some of them

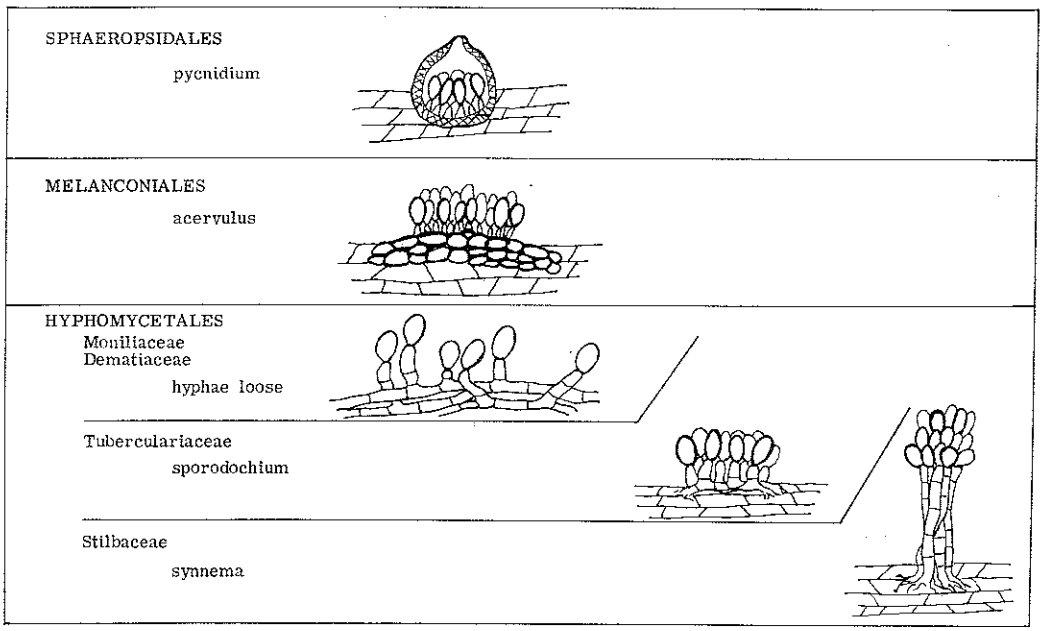

FIG. 1. FUNGI IMPERFECTI, SACCARDO CLASSIFICATION: DIAGRAMMATIC REPRESENTATION OF SUBDIVISIONS AT THE 1ST (ORDER) AND 2ND (FAMILY) LEVELS OF CHARACTERIZATION

The first two orders are defined by the relation of spores to accessory structures, the enclosing pycnidium of the Sphaeropsidales and the supporting acervulus of the Melanconiales. Spores of the Hyphomycetales are not associated with well-defined accessory structures; the order is subdivided on the basis of sporophore arrangement: loose, aggregated, or compact and vertically elongated.

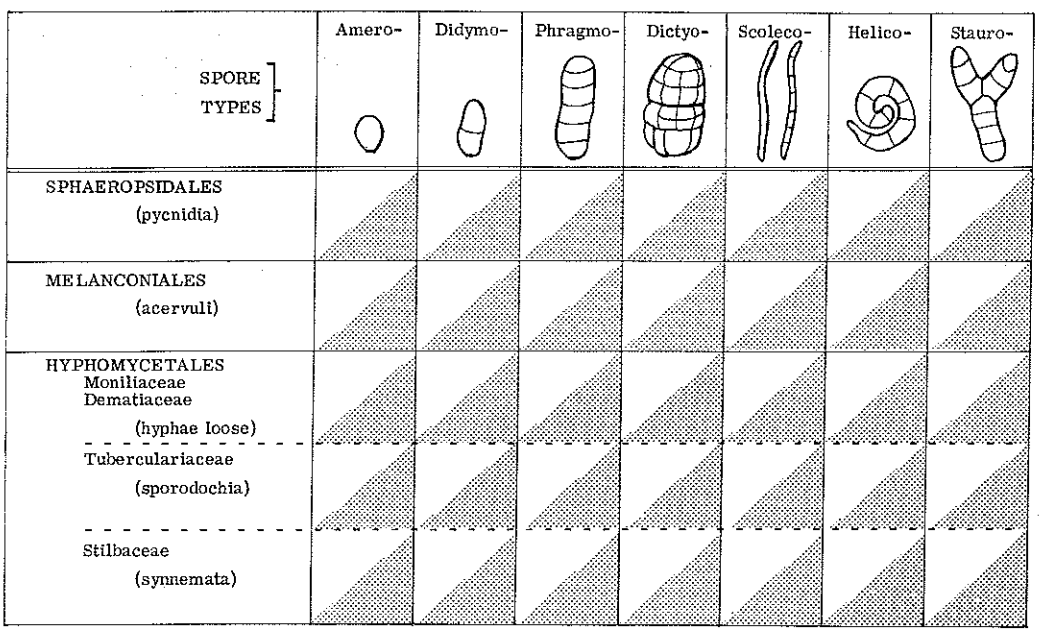

FIG. 2. FUNGI IMPERFECTI, SACCARDO CLASSIFICATION: DIAGRAMMATIC REPRESENTATION OF SUBDIVISIONS AT THE 1ST, 2ND, 3RD, AND 4TH LEVELS OF CHARACTERIZATION

Each major 1st and 2nd level category is subdivided at a 3rd level of spore and hyphal color, either hyaline or bright (clear triangles) or dark (stippled triangles), and at a 4th level of spore type. The 70 resultant categories form the pigeonhole pattern of Saccardoan systematics.

were unknown to him. However, the pigeonhole pattern was established, and most of the known imperfect fungi could be inserted in one compartment or another without too much violence. Further subdivisions, which represented genera, were based on substrate relationships and on a multitude of characters related to spore shape, ornamentation, arrangement, and accessory hyphae.

Practically all descriptive mycologists and systematists of the 19th century, including Saccardo, held the view that only the completely mature condition of a fungus, as it occurred in nature, was suitable for characterization. Studies in developmental morphology were a new field and in any case scarcely touched the lowly imperfects. Controlled culture work and genetic manipulation and interpretation have held sway only in our own times.

Saccardo and most others of his period exhibited little interest in what we now consider to be fundamental differences in the spore-production apparatus of the Fungi Imperfecti. Many of the differences were readily visible when young material was at hand, but they often were obscured in mature specimens and usually were considered to be of little consequence in classification. A body of critical information on methods of spore production has developed only within the past 30 to 40 years, and attempts to apply this information to the classification of the imperfects are so recent as to represent the new taxonomy of today.

MODERN CLASSIFICATIONS OF FUNGI

Saccardo, then, within the mycological limitations of his day, performed two remarkable services. Not only did he devise a comprehensive scheme of classification. He also made decisions on the many thousands of fungus descriptions known to him and published these opinions in a systematic fashion. We are well aware of the multiplicity of errors, misinterpretations, and inconsistencies in the Saccardoan classification; and we are becoming increasingly dissatisfied with the necessity of working within the framework of such a system in these times when so many natural relationships are being clarified and so much critical morphological and physiological information is becoming available. But we are faced with the fact, inescapable in the workaday applied aspects of mycology, that the preponderance of information in the world literature is hung on this framework of Saccardoan systematics.

Practical Operation within the Saccardoan System

The taxonomic mycologist of today, if he fulfills his responsibility of providing pertinent information on demand, has developed a bivalent systematic sense. He overlays the categories of Saccardo with interconnecting threads of new data and proceeds to pull useful information and predictions from more than one of the artificial pigeonholes. If his taxonomic interests and responsibilities are broad enough, he can operate in no other way.

Drastic revisions of the classic systematic scheme are in order — indeed, we are well convinced that they are necessary. Occasional monographs appear which emphasize a high degree of natural relationship among the organisms included; the dead wood of superficial resemblance goes into an appendix. Such monographic studies, if their yield of information is high, have the effect of a refreshing breeze; but they are tantalizingly rare. The non-mycologist may ask with impatience that we get on with the business of a new classification now that we recognize that the old ones have a low yield of information and correlation, and are cumbersome to use. The degree of such impatience can be equated only with the degree of ignorance of the problem's magnitude.

A rough comparison can be made between the number of genera currently recognized for bacteria and the number estimated for fungi. The 1957 edition of *Bergey's Manual of Determinative Bacteriology* (Breed, Murray, and Smith, 1957) offers a classification of 208 genera of Schizomycetes and Rickettsiales. The latest edition of *Ainsworth and Bisby's Dictionary of the Fungi* (Ainsworth, 1961), in contrast, lists over 9000 generic names of fungi, of which the authors accept about 4300 (the remainder being synonyms or of uncertain status). Bisby and Ainsworth (1943) have estimated a total of

100,000 species of fungi (known and as yet unknown). G. W. Martin (1951) considered this estimate excessively conservative and suggested that the number of good species of fungi is at least as great as the number of good species of higher plants, of which there are believed to be not less than 250,000. Without attempting to justify the generic and species concepts involved, the very existence of such estimates made by eminent mycologists indicates the magnitude of our classification problem.

Requirements of a New Classification System

We are agreed that some of the criteria used in the Saccardoan classification have led us to spurious relationships and, much worse, to systematic separation of naturally related organisms. What are we looking for in a system? Is it possible to identify not only the major criteria which have misguided us but also some fundamental characters which will help to set us straight?

To paraphrase the earlier quotation (p. 113) from Heslop-Harrison (1962): one of the primary functions of biological systematics is the production of a classification possessing at once the greatest possible content of information and the maximum convenience in use; an inescapable function of taxonomy is the creation of a data storage and retrieval system. Our expectations in a system must be satisfied at least in the following two areas: first, it must be comprehensive in coverage; second, the degree of yield of information must be high. There must be a place in the system for every fungus and we must be able to locate that place with some ease whenever we wish to store new information or to retrieve what already is there. Any classification which replaces or modifies that of Saccardo must do at least as well as his did in providing a niche for every known fungus.

The second major requirement of a biological classification scheme, namely, informational yield, cannot be overemphasized. Ideally, when we have placed an organism (or a group of organisms) and its complement of information in one area of the scheme, we should be able to find among its neighbors a significant amount of related information. Conversely, neighboring categories should not yield large amounts of unrelatable information. And as a corollary, groups of organisms which have large quantities of similar characteristics and informational content should not be scattered in distant areas of the system.

It is precisely this requirement of informational yield which has led to our dissatisfaction with the Saccardoan classification. Too often we have lost valuable information simply because two organisms with a great number of characteristics in common have been disposed at opposite poles of the classical scheme on the basis of a single factor of hyphal color or spore septation. Fortunately, pure culture work involving controlled environments has become a standard technique of taxonomic mycology. It no longer is necessary to base our major systematic divisions on the most obvious characters of only the mature sporulating condition. Instead, in a majority of cases we can compare any number of molds under precisely the same conditions and in all stages of their growth and development and, from these manipulations and observations, determine which characters are always held in common and which others are unstable or poorly correlated. We can divorce in cultures a dozen similar but variously categorized fungi from their dozen dissimilar hosts and substrates, and determine truly whether the categories used for these fungi are based on characters inherent in the fungi or on anomalies introduced by the host and environment. In other words, we are reaching a stage of comparative sophistication when it may be possible to recognize some fundamental characteristics among the Fungi Imperfecti and to elaborate a set of primary, secondary, and lower divisions of these organisms into a new and more meaningful classification.

It is no difficult task to find fungi which produce excellent synnemata in nature but only loose webs of mycelium in culture (e.g., some *Isaria* isolates) or others which appear as compact sporodochia on their hosts but which lose the compactness of their sporulation apparatus in culture (some *Fusarium* isolates). In these instances the three Saccardoan subdivisions of the Hyphomycetes intergrade and become untenable. Whether or not the spores are borne on a loose weft of hyphae, on a com-

pacted sporodochium, or on an erect synnema ceases to be a factor of primary systematic importance.

Does the phragmosporous *Curvularia* demand a different classification when the spores become branched? And if the spore-bearing hyphae of *Curvularia* aggregate into a synnema or are borne aloft on an erect stroma, are new systematic categories and different generic names required (Fig. 3)? Surely not; and such adherence to the major subdivisions and spore-type categories of Saccardo would do violence to an otherwise perfectly natural grouping of fungi.

What are the color limits of the multicolored *Aspergillus?* The limit is reached when the spores are black instead of brightly colored, said Spegazzini (1910) when, in deference to Saccardoan orthodoxy, he categorized the black-spored Aspergilli, including *Aspergillus niger,* in a new genus *Aspergillopsis,* systematically far-removed from its natural relatives. Not even Saccardo himself went so far in his cataloguing as to separate this natural group of molds on such flimsy grounds.

Among the several hundred isolates of dark-spored *Alternaria, Curvularia,* and *Stemphylium* maintained for my own taxonomic research there is a sprinkling of albino strains, all perfectly representative except for their lack of color. The pigeonholes of classical systematics would permit a potboiler manuscript and two or three new generic names for these natural variants, but I would lose respect for any mycologist who would publish such pseudo-Saccardoan nonsense.

Considerable emphasis has been placed thus far on the format and drawbacks of Saccardo's classification, but only because it is the single comprehensive scheme available for the Fungi Imperfecti and because to a greater or lesser degree it is used, after all, by every taxonomic mycologist.

Hughes: Conidiophores, Conidia, and Classification

Since we believe that many of the major subdivisions of classical systematics are untenable,

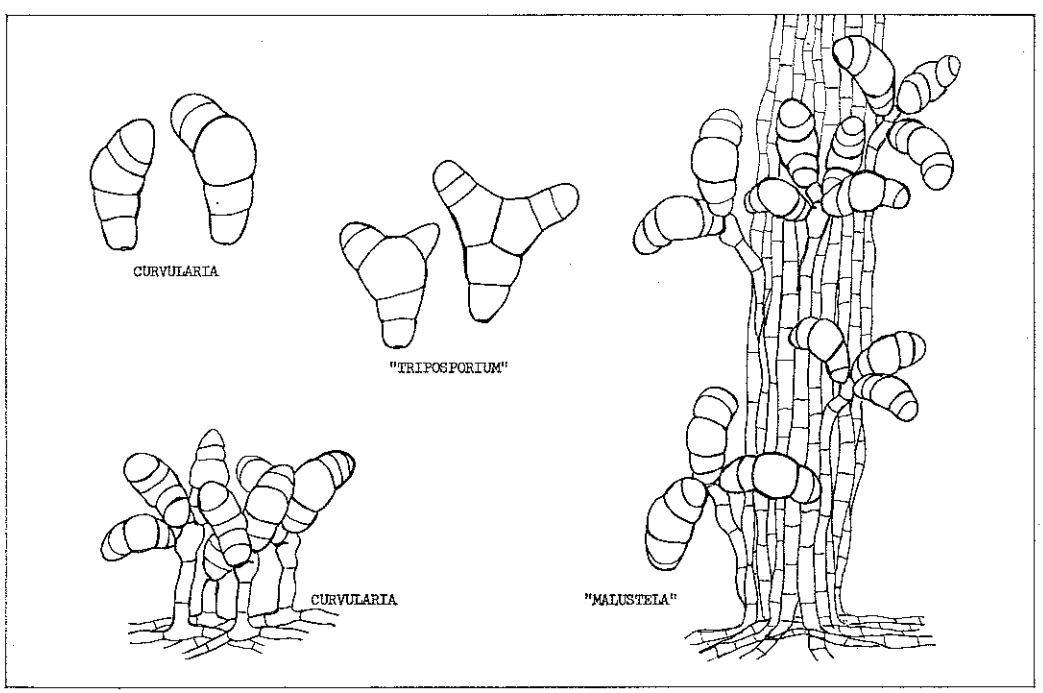

FIG. 3. *Curvularia:* DIAGRAMMATIC REPRESENTATION OF CONIDIA AND ASSOCIATED HYPHAE OF *Curvularia*

The generic labels are names which have been used for the several morphologic elaborations of these structures.

what are the alternatives? There exists at least one parallel scheme which shows great promise of leading into a natural classification of the imperfects. This scheme had its most lucid and suggestive exposition by S. J. Hughes (1953). More recent views on this scheme (Tubaki, 1958, 1963; Subramanian, 1962, 1963) are revisionary or derivative, and the classification proposed by Hughes has its own evolutionary roots in the systematized opinions of earlier mycologists (Costantin, 1888; Vuillemin, 1910a,b, 1911; Mason, 1933, 1937, 1941).

It is the thesis of Hughes "that there are only a limited number of methods whereby conidia can develop from other cells and that morphologically related imperfect states will only be brought together when the precise methods of conidium origin take first place in the delimitation of the major groupings" (p. 580). The heart of this thesis resides in the observation that any given fungus produces its asexual spores or conidia from preexisting cells in a constant manner, regardless of environmental conditions or changes. Method of spore production thus appears to be a character of first-division importance in a natural classification of the fungi. The major criteria of the Saccardoan classification — manner of grouping of conidiophores, color, and morphology of the mature spore — would be relegated to relatively minor positions. Whether or not such a major revision in our taxonomic thinking will ever bear fruit in the form of a new comprehensive classification will depend on how well it fits the several thousand imperfect fungi known, in addition to the one or two hundred used by Hughes and by others as examples.

Hughes concentrated on distinguishing eight methods of spore production among the Hyphomycetes, at the same time suggesting a ninth method and the possibility of others (Fig. 4). In seven of his sections, growth of the sporulating hypha, the conidiophore, occurs only in its apical region. In the eighth section, growth of the conidiophore occurs only at its base. The essential characteristics of the eight sections are as follows, the sections being illustrated diagrammatically in their simpler forms. The critical points for attention are (1) the precise structure or changes in structure of the conidiophore as spores are produced, and (2) the specific manner of development of spores from the conidiophore.

Section I. The conidia develop singly or in acropetal succession as blown-out ends of preexisting cells; the conidiophore itself does not increase in length (e.g., *Cladosporium, Oidium, Botrytis*).

Section II. The conidia arise as blown-out ends of the apex of the conidiophore; ends of new growing points develop at one side of the previously formed conidium, the conidiophore thus increasing in length and producing additional conidia during successive intervals of growth (e.g., *Beauveria, Brachysporium, Cercospora*).

Section III. The initial conidium arises as the blown-out end of the conidiophore apex; each additional conidium is produced as the blown-out end of the conidiophore as it elongates through the scars left on displacement of previously formed conidia. The increasing length of the conidiophore is evident in the form of this series of scars or annellations (e.g., *Scopulariopsis, Stysanus*).

Section IV. The conidia develop in basipetal series from the open apex of the conidiophore; the conidiophore, termed a phialide, does not increase in length (e.g., *Fusarium, Neurospora,* some and possibly all *Penicillium* and *Aspergillus*).

Section V. The conidia develop in gradually maturing basipetal series and originate through the meristematic nature of the apical cell of the conidiophore; the position of the conidiophore apex is fixed and it fluctuates in length only as its generative cell elongates and divides to produce a new conidium at its apex, the lower cell retaining its generative function as a conidiophore (e.g., the so-called *Oidium*-state of the powdery mildews; *Sirodesmium*).

Section VI. The conidia develop from the conidiophore protoplast as outgrowths through discrete pores in the conidiophore wall; there is no organic connection between the conidiophore wall and the wall of the developing conidium. The conidiophore may increase in length by producing a branch lateral to the older conidial pore or by growing out through the old pore (e.g., *Alternaria, Helminthosporium, Curvularia*).

Section VII. The conidia develop by the basipetal fragmentation of simple or branched

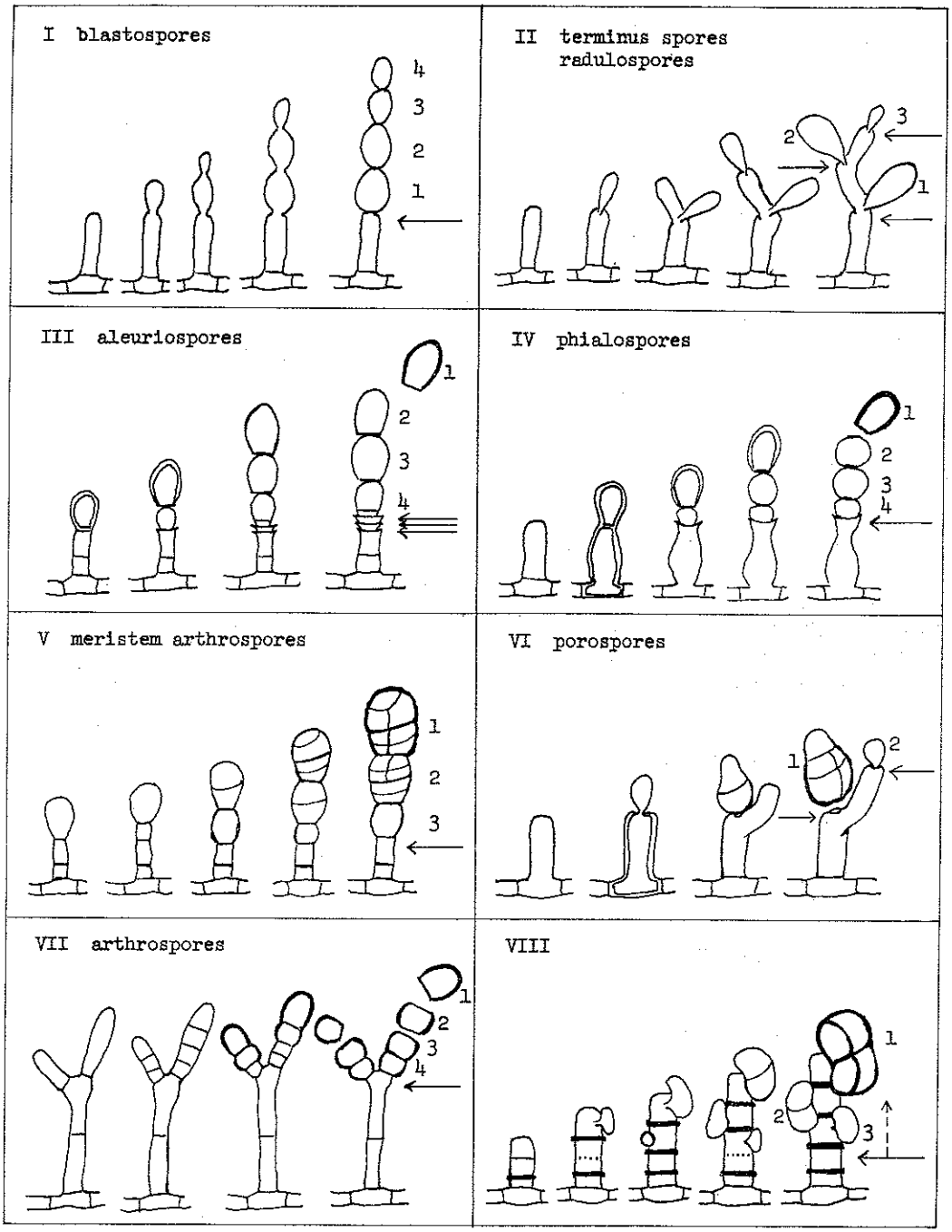

FIG. 4. FUNGI IMPERFECTI, HUGHES CLASSIFICATION: DIAGRAMMATIC REPRESENTATION OF SUBDIVISIONS AT THE FIRST LEVEL OF CHARACTERIZATION

Roman numerals correspond to the "Sections" of Hughes; Arabic numerals designate the order in which successive spores are produced; arrows indicate the regions in which spore production occurs (I-VII) or in which conidiophore elongation takes place (VIII).

hyphae; the conidiophore does not have a meristematic zone and does not increase in length during conidium formation (e.g., *Geotrichum, Actinomyces*).

Section VIII. The conidia develop from cells of a conidiophore which elongates from a basal growing point or meristematic region (e.g., *Papularia, Dictyoarthrinium*).

The reasoning involved in this proposal for new basic groupings among the Fungi Imperfecti is that the specific modes in which conidiophores develop and in which the spores are produced are absolutely fundamental to an understanding of the mature morphology of the fungi. Degrees of complexity in the arrangement of multiple conidiophores, septation and mature form of the conidia, color, ornamentation, supplementary spore forms, and physiological and ecological factors are viewed as pertinent but secondary characters useful in establishing lower-echelon systematic categories. Hughes and others, who have been interpreting this proposal, already have considerable professional response and backing, particularly from those taxonomic mycologists whose work forces them to handle living fungi and information of great diversity.

Although only a few hundred fungi have as yet been characterized in this system, we are finding already that it illuminates the relationships of many fungus groups whose natural proximity we have long recognized in practice, in spite of their artificial separation in classical systematics. However, these proposals for a basic revision in fungus systematics have not yet come close to satisfying our two major requirements in a classification, namely, comprehensive coverage and high yield of correlated information. It will require many years of intense study to characterize critically any significant portion of the imperfect fungi. And although a yield of correlated information is already promising, it will not reach practical proportions until the requirement of comprehensiveness is approached.

EVOLUTION AND ACCEPTANCE OF A NEW CLASSIFICATION OF FUNGI

Work at several levels and in many research disciplines is necessary to the evolution and acceptance of a new overall classification of the Fungi Imperfecti. The developmental morphology of great numbers of representative fungi of all degrees of complexity must be examined critically. As a corollary, there is a most urgent need for monographic studies of generic groups — studies by individuals willing not only to analyze pertinent information from all the biological and physical disciplines but also to synthesize accounts of the natural relationships of their material while discarding the illegitimate associations which abound.

The burden of effort does not lie alone with the taxonomist if we are to approximate a goal of being able to render reliable information, advice, and predictions to the many applied fields which ask for help. The burden must be shared by the geneticist, the biochemist, the phytopathologist, the medical clinician, and the industrial microbiologist. It is in our day that one mutant of one strain of one isolate of one fungus may achieve fantastic research or industrial importance. It should be in our day that the individual (or organization) who gains his reputation, grants, or wealth from the manipulation of a few mycological oddities should accept the scientific responsibility of feeding back a broader spectrum of observations than has been his custom. It is only in these ways that we can hope to achieve a comprehensive, information-rich system—our much-needed new classification.

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